

## Jumping performance of flea hoppers and other mirid bugs (Hemiptera, Miridae)

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## ABSTRACT

The order Hemiptera includes jumping insects with the fastest take-off velocities, all generated by catapult mechanisms. It also contains the large family Miridae or plant bugs. Here we analysed the jumping strategies and mechanisms of six mirid species from high speed videos and from the anatomy of their propulsive legs and conclude that they use a different mechanism in which jumps are powered by the direct contractions of muscles. Three strategies were identified. First, jumping was propelled only by movements of the middle and hind legs which were respectively 140% and 190% longer than the front legs. In three species with masses ranging from 3.4 to 12.2 mg, depression of the coxo-trochanteral and extension of femoro-tibial joints accelerated the body in 8-17 ms to take-off velocities of 0.5 to 0.8 m s<sup>-1</sup>. The middle legs lost ground contact 5-6 ms before take-off so that the hind legs generated the final propulsion. The power requirements could be met by the direct muscle contractions so that catapult mechanisms are not implicated. Second, other species combined the same leg movements with wing beating to generate take-off during a wing downstroke. In the third strategy, up to four wing beat cycles preceded take-off and were not assisted by leg movements. Take-off velocities were reduced and acceleration times lengthened. Other species from the same habitat did not jump. The lower take-off velocities achieved by powering jumping by direct muscle contractions may be offset by eliminating the time taken to load catapult mechanisms.

## INTRODUCTION

A wide range of insects across many diverse orders use just two basic mechanisms to propel jumping movements with their legs. The fastest jumpers use catapult mechanisms, as exemplified by insects such as fleas (Bennet-Clark and Lucey, 1967), locusts (Bennet-Clark, 1975), flea beetles (Brackenbury and Wang, 1995; Nadein and Betz, 2016; Schmitt, 2004) and many hemipteran plant sucking bugs (Burrows, 2003; Burrows, 2009a). The power requirements of the muscles in these jumps are beyond the maximum active contractile limits of muscle from different animals (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). To meet these requirements, the necessary energy has to be generated by the slow contractions of the muscles in advance of a jump and then stored in mechanical distortions of specialised parts of the skeleton. The sudden release of this stored energy then delivers the amplified power needed to extend the legs and launch the insect into the air at high speed. The second mechanism relies on leverage provided by direct contractions of the muscles powering movements of the propulsive legs. In general the resulting take-off velocities are lower than in catapult jumpers, but in bush crickets comparable take-off velocities are reached by the leverage given by the very long propulsive hind legs that can be more than three times body length (Burrows and Morris, 2003).

Two elaborations of these basic mechanisms occur in jumping insects. First, the number of propulsive legs is usually two, but four are used by some species. Most insects thought to use catapult mechanisms are propelled by just one pair of propulsive legs with the only known exception being snow fleas which use two pairs of legs (Burrows, 2011). The two propulsive legs, particularly when they are oriented underneath the body, as in Hemiptera, must be synchronised closely to produce an effective and directed jump. By contrast, using direct muscle contractions to produce slower movements of the legs reduces the need for synchrony. The forces generated by four propulsive legs will be distributed over a greater area reducing the energy lost to distortions of the substrate. Examples of insects using four propulsive legs include caddis flies jumping from plants (Burrows and Dorosenko, 2015b) and particular flies jumping from the surface of water (Burrows, 2013a).

The second elaboration is the addition of wing movements to the propulsive movements of the legs. In general, the very brief acceleration times of jumps propelled by catapult mechanisms, means that there is little time for wing movements to add further forces to the take-off; opening the wings may simply impede take-off by increasing drag. By contrast, the longer times to accelerate to take-off afforded by the mechanism of direct muscle contractions means that wing movements can either accompany or even precede propulsive leg movements, as, for example, in moths (Burrows and Dorosenko, 2015a) and thus provide additional thrust and lift forces.

In the suborder Auchenorrhyncha of the Hemiptera, catapult mechanisms are used to propel jumping by many species of frog-, plant-, leaf- and tree-hoppers (Burrows, 2006a; Burrows, 2007a; Burrows, 2009a; Burrows, 2013c). In the three other hemipteran suborders, only a few jumping species have been analysed in detail but all are judged to use a catapult mechanism from the measured power requirements of their jumps; in the Heteroptera one species of shore bug (Saldidae) (Burrows, 2009b), in the Coleorrhyncha, one species of *Hackeriella* (Peloriidiidae) (Burrows et al., 2007) and in the Sternorrhyncha, three species of psyllids (Pysllidae) (Burrows, 2012).

The widespread use of catapult mechanisms for jumping in the Hemiptera revealed in this series of examples, raises the question of whether the second mechanism of jumping powered by direct muscle contraction has evolved at all in this order. An analysis was therefore made of the plant bugs (also called capsids or mirid bugs) which belong to a large family (Miridae) within the Heteroptera of more than 11,000 species worldwide (Cassis and Schuh, 2012) including about 200 in the UK (Dolling, 1991). Some live in the same habitats as the catapult-powered frog-, plant- and leaf hoppers. This paper shows that particular species of mirid do jump, but that they use a leverage mechanism powered by direct contractions of muscle. Take-off velocities are low and do not require a catapult mechanism dependent upon power amplification and energy storage. The middle and hind pair of legs can provide the sole propulsion, but in some species wing movements may also contribute. In other species jumping propelled by the legs does not seem to be a part of their locomotory repertoire and instead wing movements alone suffice to generate a slow take-off.

## MATERIALS AND METHODS

Mirids (family Miridae) belong to the order Hemiptera, sub-order Heteroptera. They were collected in three locations. First, adult male and female *Phytocoris varipes* Boheman, 1852 were found in a wet meadow at Wells-next-the-sea, Norfolk, UK in late August 2010 - 2015. Second, female *Microtechnites bractatus* (Say, 1832) (formerly *Halticus bractatus*, see revision of the *Halticini* (Tatarnic and Cassis, 2012), male and female *Orthocephalus saltator* (Hahn, 1835), *Stenotus binotatus* (Fabricius, 1794) and *Plagiognathus* sp. were caught around Halifax, Nova Scotia, Canada in 2015. Third, male and female *Psallus perrisi* (Mulsant and Rey, 1852) were found in Girton, Cambridge, UK in 2015, as were further specimens of *S. binotatus*. All specimens of these species were macropterous (fully winged) with the exception of one individual male *Phytocoris varipes* and one *O. saltator* which were brachypterous (short-winged). These two individuals were not included in the analysis of jumping performance.

Photographs of live mirids were taken with a Nikon D90 camera fitted with a 100 mm Nikon macro lens. The morphology of the legs was examined in intact insects, and in those fixed and stored in 70% alcohol, or 50% glycerol. To measure the lengths of the legs, images of fixed specimens were captured with a GXCAM-5C digital camera (GT Vision, Haverhill, Suffolk, UK) attached to a Leica MZ16 microscope (Wetzlar, Germany) and projected onto a large monitor. Images of individual leg segments (trochanter, femur, tibia and tarsus) were then measured against a ruler and the sum of these parts gave the length of a particular leg to an accuracy of 0.1 mm. Body masses were determined to an accuracy of 0.1 mg with a Mettler Toledo AB104 balance (Beaumont Leys, Leicester, UK).

Sequential images of jumps were captured at a rate of 1000 s<sup>-1</sup> or 5000 s<sup>-1</sup> and with an exposure time of 0.2 and 0.1 ms respectively, with a Photron Fastcam 1024PCI high speed camera (Photron (Europe) Ltd, West Wycombe, Bucks., UK). Images from the camera were fed directly to a computer. The larger *P. varipes* were free to jump in a glass chamber 80 mm wide, 80 mm tall, and 10 mm deep at floor level and widening to 25 mm at the top; the smaller species jumped in a chamber 30 mm wide, 25 mm tall, and 10 mm deep. The floor of each chamber was made of 12 mm thick, closed

cell foam (Plastazote). The camera pointed at the centre of a chamber, the shape of which meant that most jumps were in the image plane of the camera. Jumps that deviated to either side of this plane by  $\pm 30^\circ$  were calculated to result in a maximum error of 10% in the measurements of joint or body angles. Sequences of images were analysed with Motionscope camera software (Redlake Imaging, Tucson, AZ, USA), or with Canvas 14 (ACD Systems International, Seattle, WA, USA). To allow different jumps to be aligned and compared, the time at which the hind legs lost contact with the ground and the insect became airborne was designated as  $t = 0$  ms. The time at which the hind legs started to move and propel the jump was also determined and the interval between these two events therefore defined the period over which the body was accelerated. Peak velocity was calculated as the distance moved in a rolling 3 point average of successive frames. Photographs and anatomical drawings were made from both live and preserved specimens. The results are based on 182 jumps by 39 mirids at temperatures of 20 - 22° C. Seventy nine of these jumps were analysed in detail (Table 2). Measurements are given as means  $\pm$  standard error of the mean (s.e.m.) for an individual insect and as mean of means for a particular species.

## RESULTS

### Shape of body and legs

All of the species collected that were either observed to jump in the field, or were suspected of doing so, had similar body shapes characterised by antenna that were prominently jointed and could be longer than the body (Fig. 1A,B). They also had long piercing mouthparts that extended posteriorly and ventrally, in some species beyond the articulations of the hind legs (Fig. 1B). In the smallest species that jumped, *Microtechnites bractatus*, females had a mass of  $3.4 \pm 0.7$  mg and a body length of  $2.7 \pm 0.03$  mm (N=4) (Table 1). In the largest species that jumped, *Phytocoris varipes*, females had a mass of  $12.2 \pm 0.6$  mg and a body length of  $6.4 \pm 0.1$  mm (N=5); whereas the comparable figures in males were  $7.9 \pm 0.04$  mg and  $5.6 \pm 0.3$  mm (N=5); both measurements are significantly different (t-test:  $t_6 = -5.020$ ,  $P = 0.002$ ).

The hind legs of all the species, subsequently shown in the laboratory to jump, were 180 to 190% the length of the front legs and 150 to 190% the length of the body. The middle legs were only 110-120% the length of the front legs and about the same length as the body. The increased length of the hind legs was attributable mainly to the femora which were 182% and 197% (respectively in *Phytocoris varipes* and *M. bractatus*) of the length of the front legs, and to the tibia which were 117% and 128% longer (Fig. 1C,D). The width of a hind femur in *Phytocoris varipes* was twice that of a front femur and in *M. bractatus* was even wider at 2.3 times (Fig. 1C,D). Relative to the cube root of body mass, the length of the hind legs of all jumping species had ratios ranging from 3.3 to 5.5 (Table 1). By contrast, in *Psallus perrisi*, which were never observed to jump either in the field or laboratory, the hind legs were relatively shorter than those of the jumping species; their entire length was only 140% that of the front legs and just 88% that of the body (Table 1).

### Kinematics of jumping

Across all mirid species that were analysed, three distinct strategies for launching into the air were seen. First, propulsion was applied by movements of the middle and hind legs while the wings played no part and remained folded over the body. This strategy was used by *Phytocoris varipes*, *M. bractatus* and *O. saltator* so that the whole of their

movements from take-off until landing were entirely dependent on the propulsion provided by the legs. Only rarely did the wings open and begin to flap once the insect was airborne to provide a transition to powered flight. Second, were jumps by different species in which the same pattern of leg movements was used in combination with movements of the wings that preceded take-off. Third, were take-offs in still further species that involved no changes in the joint angles of the middle and hind legs and were thus inferred to be propelled by flapping movements of the wings.

To understand the propulsive movements of the legs, jumps were first analysed in the largest species, *Phytocoris varipes*, in which images of jumps were captured at  $5000\text{ s}^{-1}$  from a side view (Fig. 2, Supplementary material, Movie 1) and from underneath (Fig. 3, Supplementary material, Movie 2). From these images the details and sequence of movements of particular leg joints could be plotted (Fig. 4). The front legs did not move in a consistent pattern from jump to jump that would indicate a contribution to the generation of thrust. Instead their movements raised or lowered the angle of the body relative to the ground and provided support while jumps were propelled by movements of the middle and hind pairs of legs. Neither the middle or hind pairs of legs were moved into the same position before the start of their propulsive movements for a jump. The hind legs were usually levated about the coxo-trochanteral joint but not always into their most extreme position. Similarly the hind and middle femoro-tibial joints were never observed to be fully flexed before a jump. The propulsive leg movements could therefore be generated from different starting angles of these joints. In insects that use a catapult mechanism for jumping, the propulsive legs are always moved into the same starting position. This is therefore the first indication that these mirids may not use a catapult mechanism.

The first detectable movements of the propulsive middle and hind legs were those of the trochanter depressing about the coxa. This was seen most readily when jumps were viewed from underneath (Fig. 3), or when viewed from the side, as a movement of the femur (to which the trochanter is closely linked) relative to the horizontal or the long axis of the body (Fig. 2). These initial movements of the middle and hind legs occurred within 1 ms of each other and the subsequent period until the insect became airborne represented the acceleration phase of the jump. The depression of the coxo-trochanteral joints was accompanied by extension of the femoro-tibial joints. About 5 to 6 ms before take-off, the shorter middle legs lost contact with the ground while the hind legs continued to depress and extend until they too left the ground at which point the insect became airborne (Fig. 2). For the last part of this acceleration phase of the jump, only the hind legs were able to provide any propulsion.

This sequence of movements by the hind legs and the coxo-trochanteral joints of the middle legs characterised the vast majority jumps by *Phytocoris varipes* (Fig. 4A,B). In some jumps, however, the femoro-tibial angles of the middle legs changed little as the insect was propelled upwards and forwards (Figs 2, 4C). This suggested that the middle legs were contributing little propulsion relative to the hind legs. By contrast, in some other jumps it was possible to see small particles being displaced as the middle legs exerted force against the ground. In a further few jumps, the two middle legs depressed and extended fully whilst the two hind legs were still moving into their starting position by levating and flexing. The forward and upward movement of the body during this time could thus be attributed entirely to the thrust of the middle legs.

Analyses of jumps by *M. bractatus* as illustrated by views from the side (Fig. 5, Supplementary material, Movie 3) or underneath (Fig. 6), and by *O. saltator* in a view



from behind (Fig. 7, Supplementary material, Movie 4) indicate that both these closely related species (Subfamily Orthotylinae, Tribe Halticini) use the same pattern of leg movements for propulsion, as described above for *Phytocoris varipes*. In preparation for jumping, none of the legs moved to the same starting position before a jump was initiated. All jumps were propelled by the combined movements of the middle and hind pair of legs, with the critical angular changes occurring at the coxo-trochanteral and femoro-tibial joints (Fig. 8). In the hind legs, changes in these joint angles followed a consistent pattern in different jumps (Fig. 8 A,B). By contrast, the changes in the joint movements in the middle legs, particularly of the femoro-tibial angles, were less marked and less consistent (Fig. 8C). The middle legs were always the first to reach the limits of movement at these joints and then lost contact with the ground. The longer hind legs alone then provided the thrust during the latter part of the acceleration phase of a jump and take-off occurred when they lost contact with the ground.

## Jumping and wing movements

All jumps by *Phytocoris varipes*, *M. bractatus* and *O. saltator* were propelled solely by the movements of the middle and hind legs without the wings moving from their folded position over the body before the insect became airborne. In two jumps (3%) by *Phytocoris varipes* the wings were opened once airborne, but in the other two species no such wing movements were recorded even after take-off.

Wing movements were, however, used before take-off in other mirids. In *Plagiognathus sp.*, a quarter of all take-offs were propelled by a combination of leg movements and wing movements. In these jumps the wings opened before the middle and hind legs started their propulsive movements. In the jump illustrated (Fig. 9, Supplementary material, Movie 5), the leg movements began 8 ms before take-off. At that time the wings also began to depress and executed a full wing beat cycle, so that they were depressing again at take-off. This jump thus led seamlessly into powered flapping flight.

By contrast, in all recorded take-offs by *S. binotatus*, the wings were opened and began to beat before take-off. In some of these take-offs, the joint angles of the middle and hind legs did not change in a way commensurate with the generation of forward or upward thrust. For example, the angles of the coxo-trochanteral and femoro-tibial joints of the hind legs did not change until the tarsi had lost contact with the ground and the insect had become airborne (Fig. 10). Instead the wings executed a few wingbeat cycles before take-off; in the example shown, take-off occurred during the depression movement of the fourth wingbeat cycle (Fig. 10).

## Jumping performance

The jumping performance of the different mirids was calculated from the kinematics of their jumps (Table 2). In *Phytocoris varipes*, the heaviest species analysed, the acceleration time was  $15.7 \pm 1.2$  ms in 16 jumps by 4 males and  $17.2 \pm 1.9$  ms in 14 jumps by 4 females (Table 2). There was no significant difference in the values between males and females (t-test:  $t_6 = -0.686$ ,  $P = 0.519$ ). In the lightest species *M. bractatus*, the acceleration time was shortest at  $8.7 \pm 1.1$  ms ( $N = 6$  insects) and in *O. saltator* was intermediate at  $10.7 \pm 0.9$  ms ( $N = 3$ ). In all of these species their jumps were propelled only by movements of the legs (Figs. 2,3,5-7). In *Plagiognathus sp.* in which combined movements of the wings and legs were used to effect take-off (Fig. 9), the acceleration time was  $9.5 \pm 0.4$  ms ( $N = 16$  insects), even though their body mass at  $2.2 \pm 0.3$  mg was the lowest of all mirids analysed. In *S. binotatus* in which a

few cycles of wing beats alone propelled take-off, the acceleration phase measured from the first elevation of the wings until take-off could be as high as 39 ms (Fig. 10).

The mean of means take-off velocity was  $0.8 \text{ m s}^{-1}$  in both male and female *Phytocoris varipes*, with the best jumps reaching  $1 \text{ m s}^{-1}$  (Table 2). There was no significant difference between these values of take-off velocity in males and females (t-test:  $t_6 = 0.503$ ,  $P = 0.633$ , 16 jumps by 4 males and 14 jumps by 4 females). In *M. bractatus* and *O. saltator* the mean of means take-off velocities of each was  $0.5 \text{ m s}^{-1}$  with the fastest jumps reaching  $0.8$  and  $0.6 \text{ m s}^{-1}$  respectively. In the species which used leg and wing movements, the take-off velocity was the lowest at only  $0.4 \text{ m s}^{-1}$ . The angle of the body relative to the horizontal at take-off ranged from  $24.2$  to  $46.2$  degrees. The take-off trajectory of the different species had a greater range of  $25.6$  to  $76.1$  degrees. In male and female *Phytocoris varipes* there was no significant difference in either the body angle at take-off (t-test:  $t_6 = 0.400$ ,  $P = 0.703$ , 16 jumps by 4 males and 14 jumps by 4 females), or in the angle of the take-off trajectory (t-test:  $t_6 = 0.221$ ,  $P = 0.296$ ).

The energy requirements for jumping were highest at  $3.9 \text{ } \mu\text{J}$  in the heaviest female *Phytocoris varipes* and lowest at  $0.2 \text{ } \mu\text{J}$  in the lightest species, *Plagiognathus* sp. (Table 2). Acceleration ranged from  $43$  to  $61 \text{ m s}^{-2}$ , rising to  $99$  in the best jump by a female *Phytocoris varipes*. Forces of  $4\text{--}6 \text{ g}$  were experienced, rising to  $14 \text{ g}$  in the best jump by *M. bractatus*. From the calculations of power and energy, it was estimated that the fastest jumps in the different species required a power output of  $198\text{--}547 \text{ W kg}^{-1}$  of muscle, on the assumption that the muscles powering the propulsive movements of the middle and hind legs comprised approximately 10% of body mass. Such relative muscle masses have been measured in other insects that use the hind legs alone to propel jumping (Burrows, 2006a; Burrows and Bräunig, 2010). The use of two pairs of propulsive legs by mirids should increase the available mass of jumping muscle, indicating that the estimated power requirements per kg muscle would therefore be lower.

## DISCUSSION

Take-off in three species of mirids, *M. bractatus*, *O. saltator* and *Phytocoris varipes*, could be propelled solely by movements of the middle and hind legs with the wings remaining closed. In these jumps, the middle legs always lost contact with the ground first so that the hind legs provided the only propulsion during the latter part of the acceleration phase. In *Plagiognathus* sp. the propulsive movements of the legs were accompanied by flapping movements of the wings and in *S. binotatus*, jumps were apparently propelled by the movements of the wings alone. Other species such as *Psallus perissi* were not observed to jump in the field or the laboratory. The jumping species had hind legs that were proportionately longer than those in non-jumping species relative to the front legs and to the length of the body. The femora of the hind legs in jumping species were also up to 2.3 times wider than those of the front legs reflecting a larger volume to accommodate the muscles extending the femoro-tibial joints.



## Jumping is propelled by direct muscle contractions

Calculations from the kinematics of the jumps performed by the mirid species analysed here suggest that the power requirements for jumping can be met by direct contractions of the muscles that move the middle and hind legs. In many different animals the contractile limits of muscle range from 250 to 500 W kg<sup>-1</sup> muscle (Askew and Marsh, 2002; Ellington, 1985; Josephson, 1993; Weis-Fogh and Alexander, 1977). Only in jumps of mirids with the fastest take-off velocities did the power requirements (198–547 W kg<sup>-1</sup>) approach the upper limits of what muscle could therefore be expected to deliver. By contrast, similar estimations of the power requirements for jumps in the shore bug *Saldula saltatoria*, the only other jumping bug in the Heteroptera so far analysed, gave values that were about ten times higher at 4,500 W kg<sup>-1</sup> muscle (Burrows, 2009b). In planthoppers and froghoppers estimated values are even higher and can exceed 100,000 W kg<sup>-1</sup>. Figures of this magnitude imply that a catapult mechanism must be used in which energy is generated by the slow contraction of muscles and stored in mechanical distortions of the skeleton before being released suddenly to power the rapid leg movements. The best take-off velocities in shore bugs were twice as high as in even the smallest mirids and were reached in acceleration times that were half as long. Catapult mechanisms have also been implicated to explain the jumping performance of a Coleorrhynchan bug (Burrows et al., 2007), of Sternorrhynchan jumping plant lice (Burrows, 2012) and of all the Auchenorrhynchan species so far analysed (Table 3). For froghoppers and planthoppers which belong to the last group, these inferences have been confirmed by recordings from muscles during jumping (Burrows, 2007b; Burrows and Bräunig, 2010). Such recordings indicate that the muscles contract for long periods (often several seconds) before the legs are suddenly released to power a jump which is then completed in less than 1 ms.

The use of direct muscle contractions to propel jumping and take-off in mirids is supported by three further findings. First, mechanical devices have not been found that could restrain the legs should contractions of the muscles precede the propulsive jumping movements. This is in contrast to froghoppers, for example, where a protrusion covered in microtrichia is present on a hind coxa which engages with a similar protrusion on a hind femur before the release of the rapid propulsive movements of the hind legs (Burrows, 2006b). Similarly there appear to be no mechanical devices in the legs or thorax that could store energy in their distortions prior to the release of a jump, and which are associated with the presence of the elastic protein resilin (Andersen and Weis-Fogh, 1964). Second, the propulsive movements of the middle and hind legs did not start from the same position in different jumps. By contrast, locking the legs in the same starting position is a pre-requisite for engaging the mechanics of a catapult mechanism; for example, froghoppers fully levate both hind trochantera about their coxae and grasshoppers fully flex their tibiae about their femora. Third, if the jumps were to be propelled by catapults, all four participating legs would have to be closely synchronised and no such mechanism that could do this has been found. Snow fleas are the only example of insects thought to use a catapult mechanism distributed across four legs. In these insects, each leg has a potential site for the storage of energy associated with the presence of resilin and located in a similar position to that used by fleas (Bennet-Clark and Lucey, 1967; Lyons et al., 2011; Sutton and Burrows, 2011).

How does the performance of mirids analysed here compare with other insects that use the same mechanism of direct muscle contractions, and with those insects that use a

catapult mechanism? Three stark distinctions are revealed if 32 species of jumping insects from 12 orders are divided into two groups according to these two mechanisms for jumping: a group which is thought to use direct muscle contractions and a group which is thought to use a catapult mechanism (Table 3). First, time to accelerate the body to take-off is longer in the jumps of insects powered by direct muscle contractions compared to those which use a catapult mechanism. Acceleration times in mirids ranged from 9 to 17 ms and in insects also using the same mechanism can be as long as 100 ms. By contrast, in small insects that use a catapult mechanisms acceleration times are much lower, ranging from less than 1 ms to a few milliseconds. Second, insects that use direct muscle contractions achieve lower take-off velocities than those using a catapult mechanism. Mirids have take-off velocities of 0.5 to 1 ms<sup>-1</sup> whereas froghoppers and planthoppers that use a catapult achieve take-off velocities of 4.7 and 5.5 ms<sup>-1</sup> respectively. Third, the power output required for the best jumps using direct muscle contractions, is within the measured values for muscle from many animals. By contrast, for insects using a catapult mechanisms the required power output can be many times greater than muscles could deliver in the short acceleration times available.

There are just four known outliers to these generalisations. First, bush crickets that jump by using direct contractions of muscle can reach take-off at velocities which match those of insects using a catapult mechanism (Burrows and Morris, 2003). This is achieved by the enormous leverage produced by their very long hind legs. Second, the fly *Hydrophorus albofloreus* requires a power output that is higher than could be produced by direct contractions of the small leg muscles, but a catapult mechanism is not implicated. Instead, jumps of this fly from the surface of water are produced by the propulsive movements of the hind and middle legs combined with flapping movements of the wings, or by movements of the wings alone (Burrows, 2013a). Third, the power requirements of jumps by snow fleas (*Boreus hyemalis*) are at the top end of the capabilities of muscle and might thus be met by direct muscle contractions (Burrows, 2011). The reason for proposing that they use a catapult mechanism lies in the insensitivity of jumping performance to temperature – these insects jump around on snow – and in the presence of potential energy stores for each of the four propulsive legs. Fourth, large insects such as locusts, stick insects and bush crickets all have long legs so that the time taken to extend them fully would be longer whichever mechanism were used.

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## COMPETING INTERESTS

No competing interests declared.

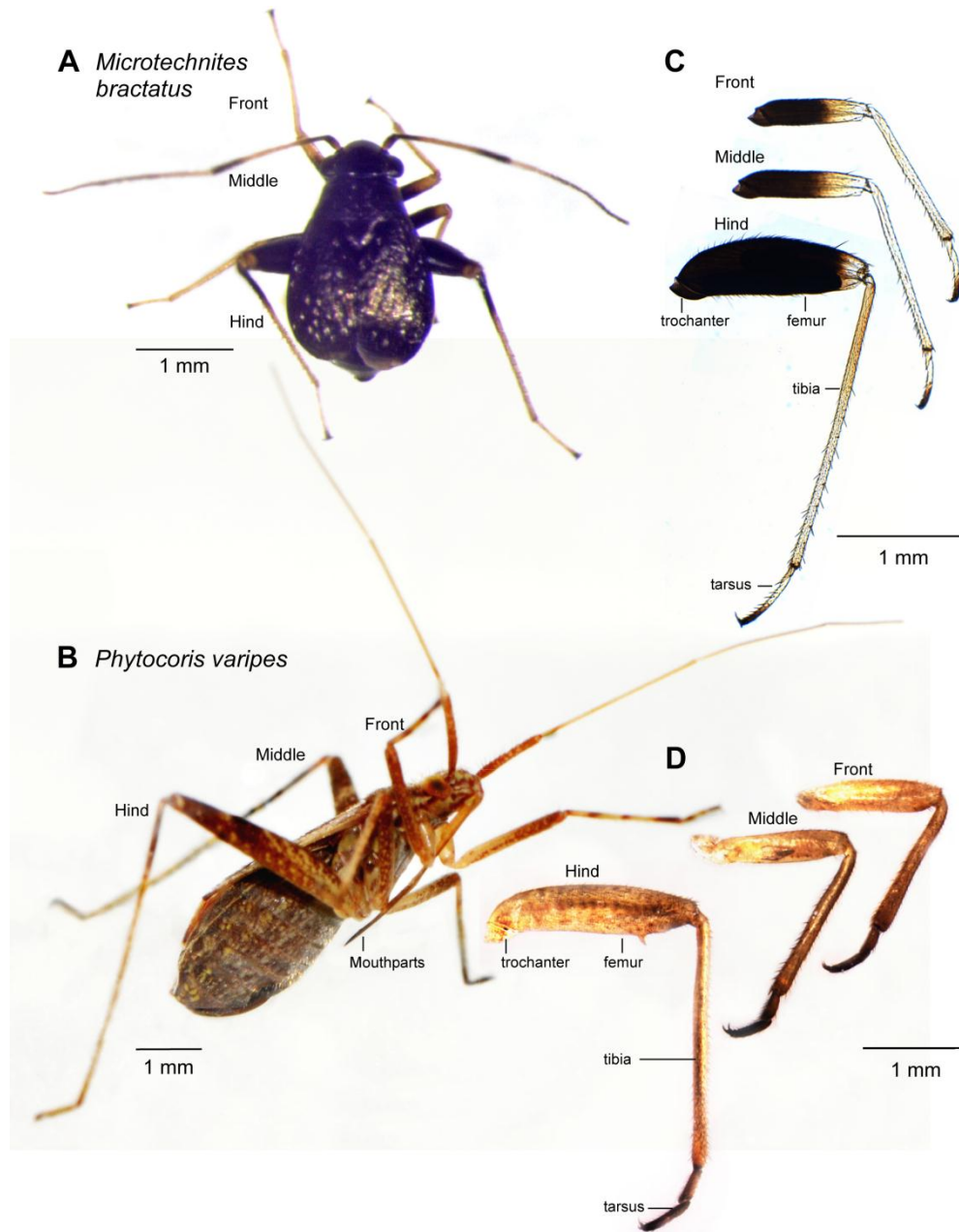
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## AUTHOR CONTRIBUTIONS

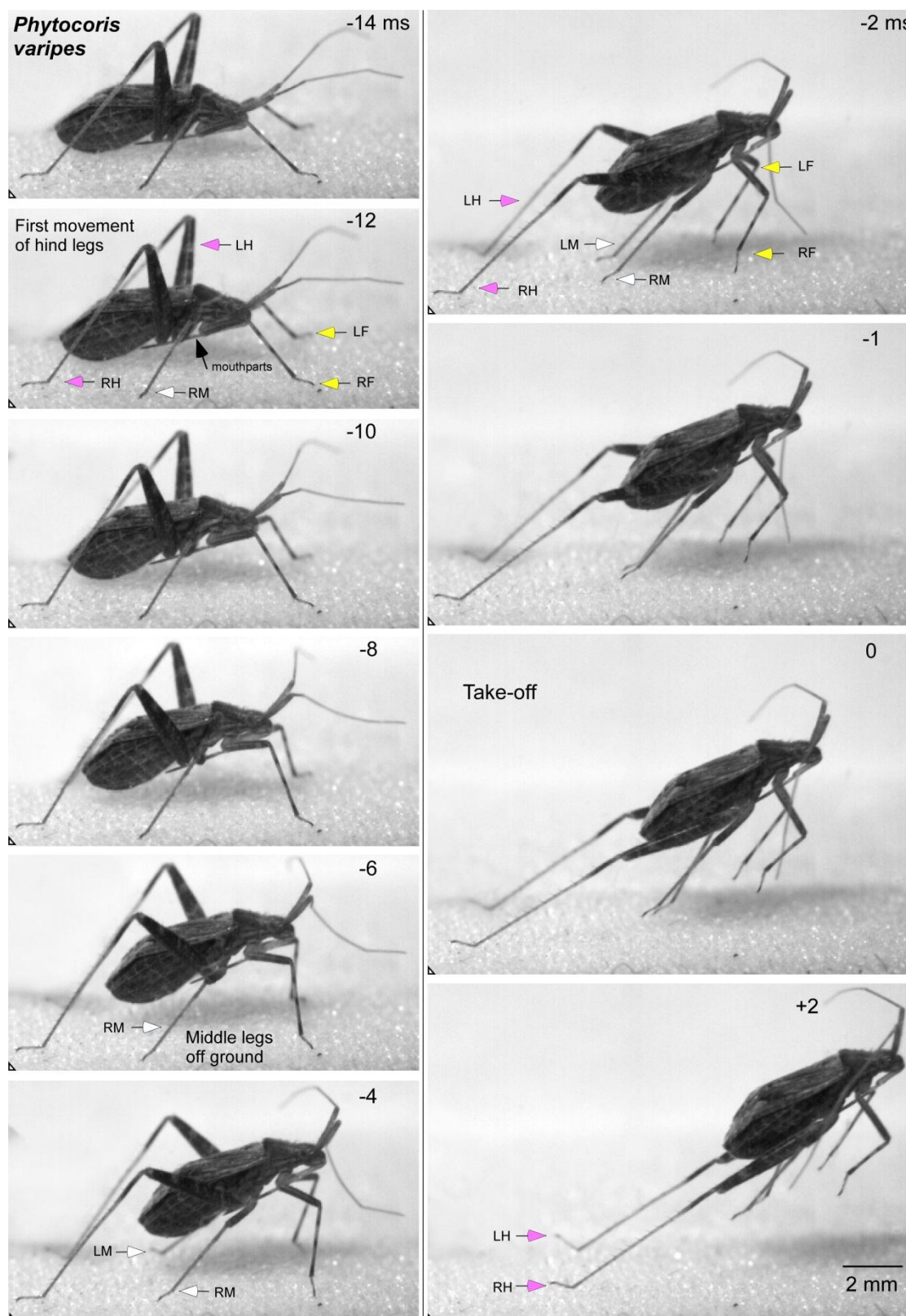
M.B. initiated the project, collected the insects, videoed the jumping behaviour, carried out the kinematic analyses, and wrote the first draft of the paper. M.D. analysed the jumping performance from the videos and co-wrote the paper.

## Figures



**Fig. 1**

**Body form of mirids as related to jumping.** (A) Photograph of the smallest mirid analysed, a female, macropterous *Microtechnites bractatus* viewed dorsally. (B) Side view of the largest mirid analysed, a female, macropterous *Phytocoris varipes*. (C) The left legs of *M. bractatus* viewed laterally. (D) The left legs of *Phytocoris varipes* viewed laterally.

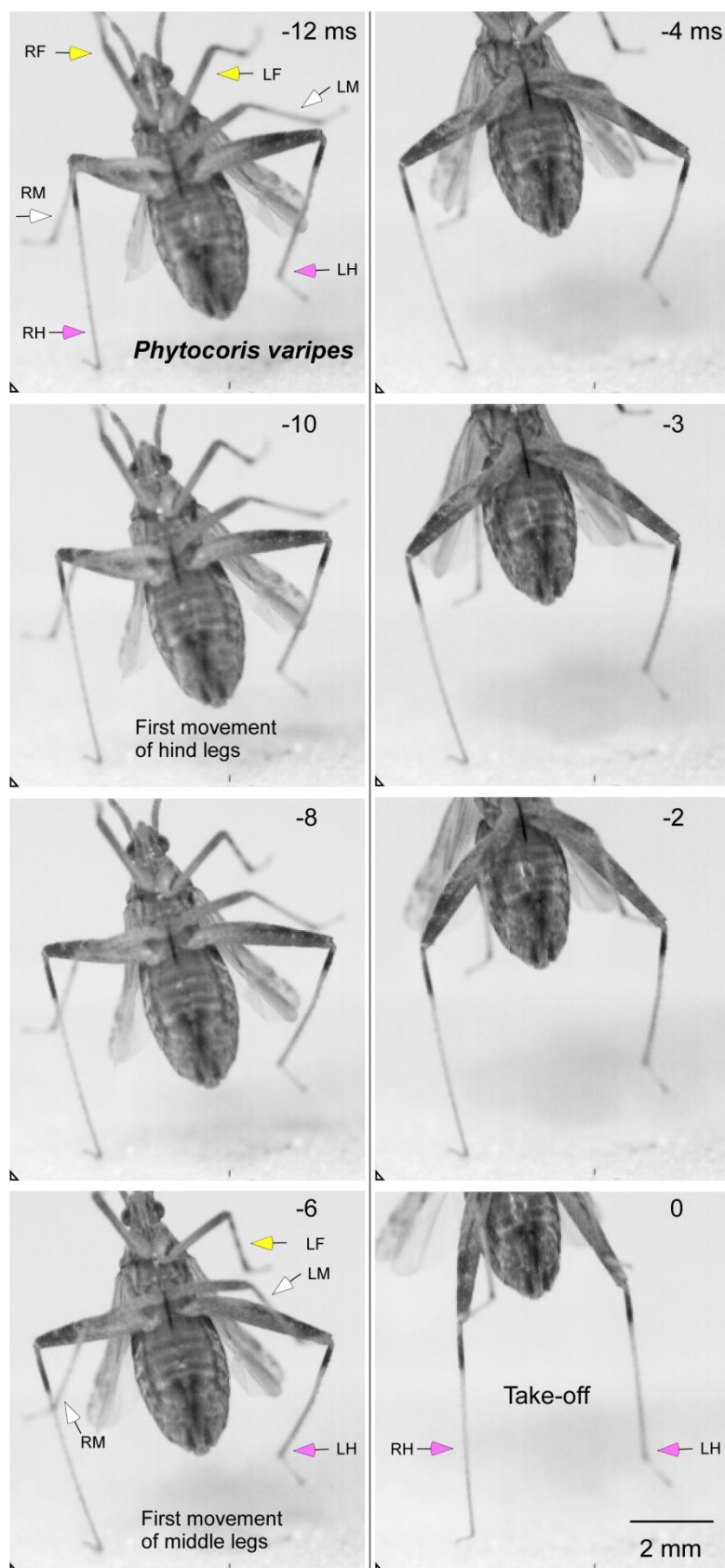


**Fig. 2**

**Jump by a female, macropterous *Phytocoris varipes* from the horizontal and viewed from the side.** The hind legs were the first to move and the last to lose contact with the ground. The middle legs were also depressed and extended but lost contact

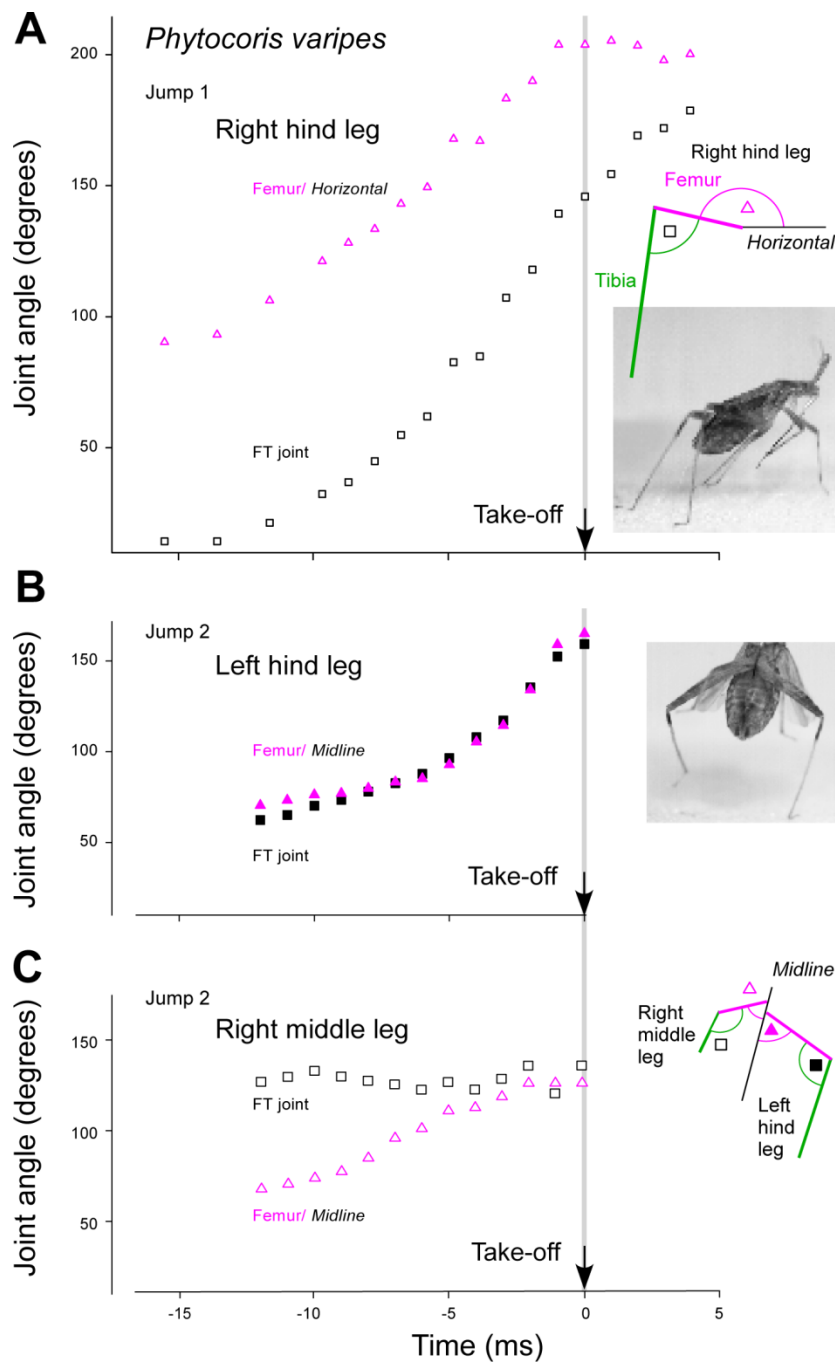
with the ground (frame -6 ms) before take-off. Images were captured at  $5000\text{ s}^{-1}$  and with an exposure time of 0.1ms and are arranged in two columns with the timing of the frames given relative to take-off at time = 0 ms. In this and Figures 3, 5-7, 9-10, the front legs (LF, left front; RF, right front) are indicated by arrows with yellow heads, the middle legs (LM, RM) by arrows with white heads and the hind legs (LH, RH) by arrows with pink heads. The triangles in the bottom left hand corners of each image indicate a constant spatial reference point.





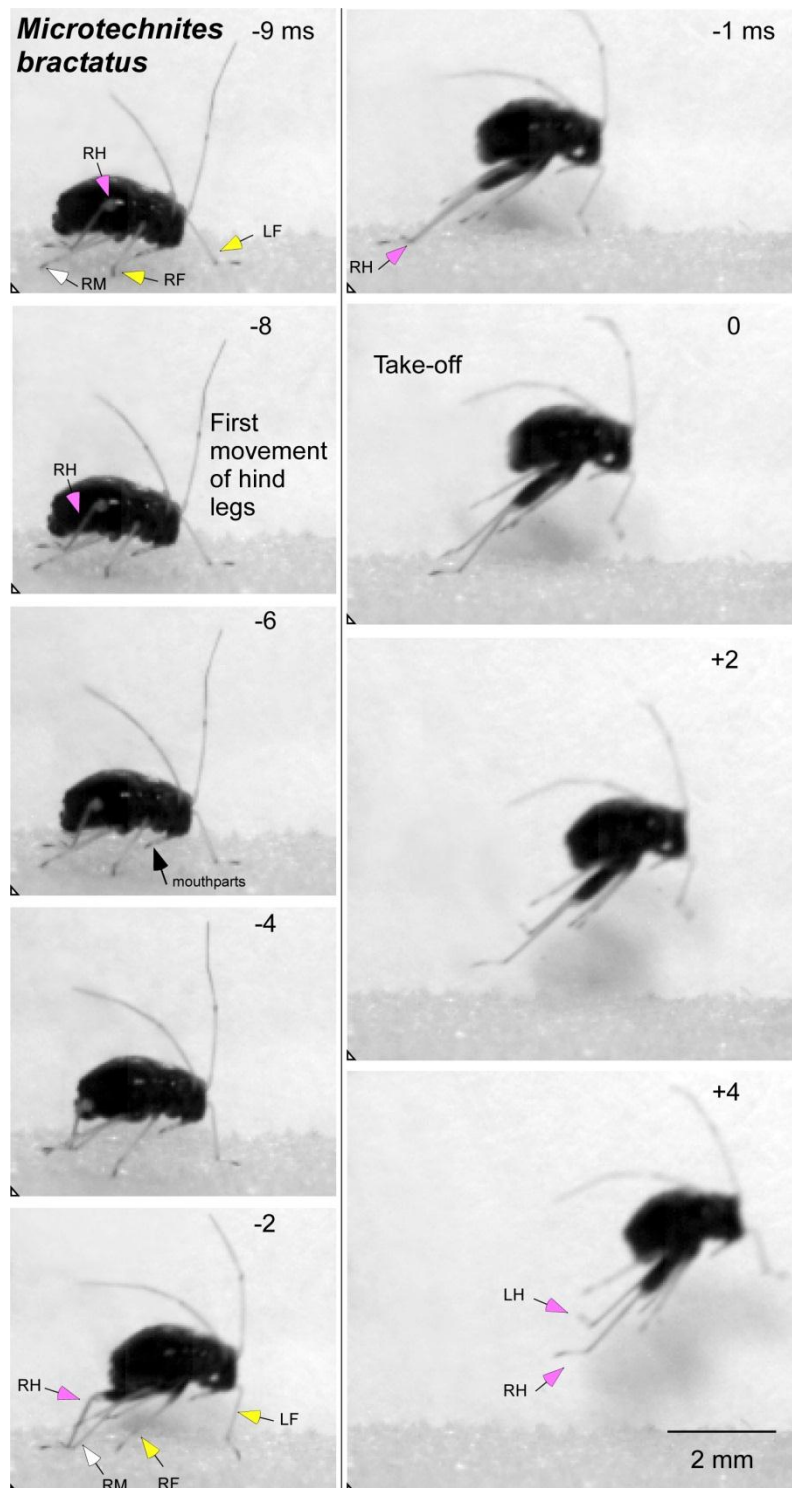
### Fig. 3

**Jump by a male, macropterous *Phytocoris varipes* viewed from underneath.** The hind legs move first followed 4 ms later by the middle legs. The fully depressed and extended hind legs are the last to leave the substrate. The wings were open during the jump but were not moved. Images were captured at  $5000\text{ s}^{-1}$  and with an exposure time of 0.1 ms.



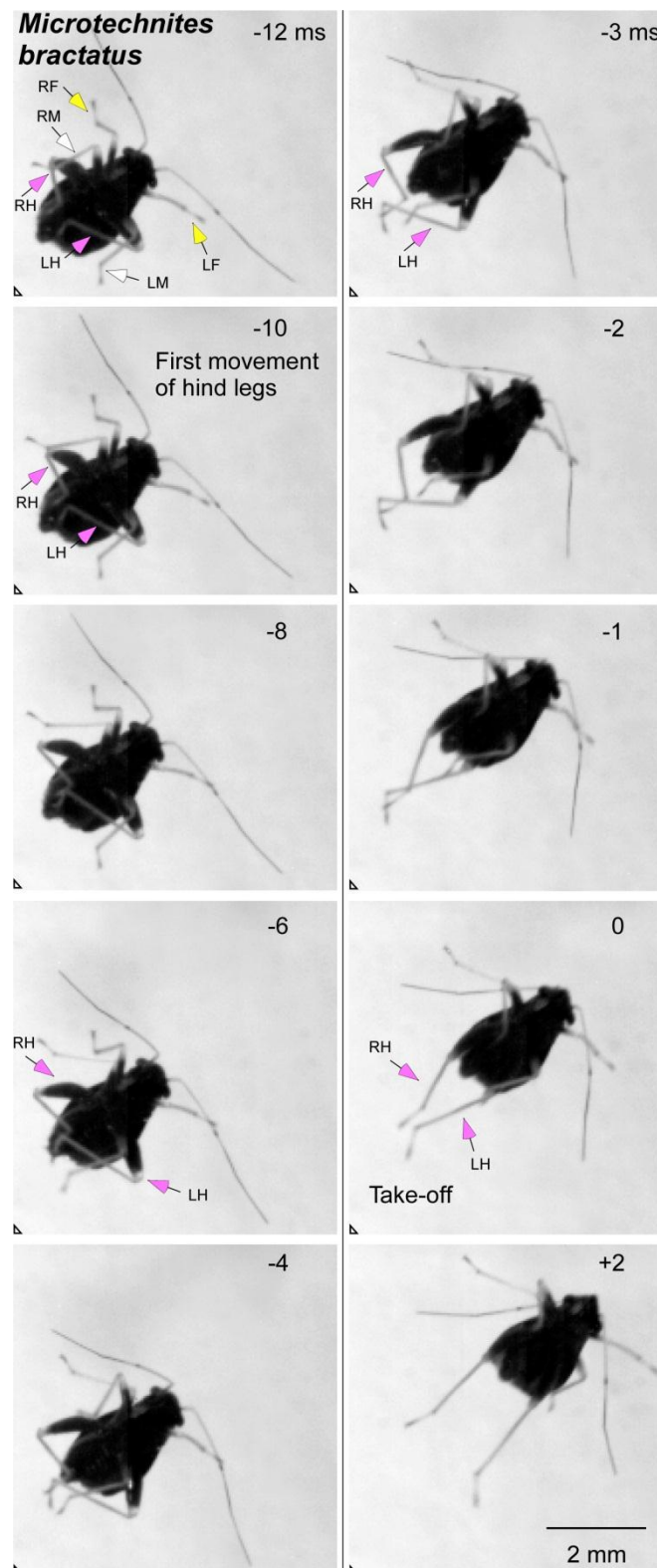
**Fig. 4**

**Changes in joint angles of the propulsive legs during jumps by *Phytocoris varipes*.** (A) Side view of jump 1 in which the depression of the right hind femur and extension of the right hind tibia are plotted. (B,C) Ventral view of jump 2 in which the angular changes of the same joints in the left hind (B) and right middle leg (C) are plotted. The inset frames from the two jumps and the stick diagrams indicate how the angles were measured.

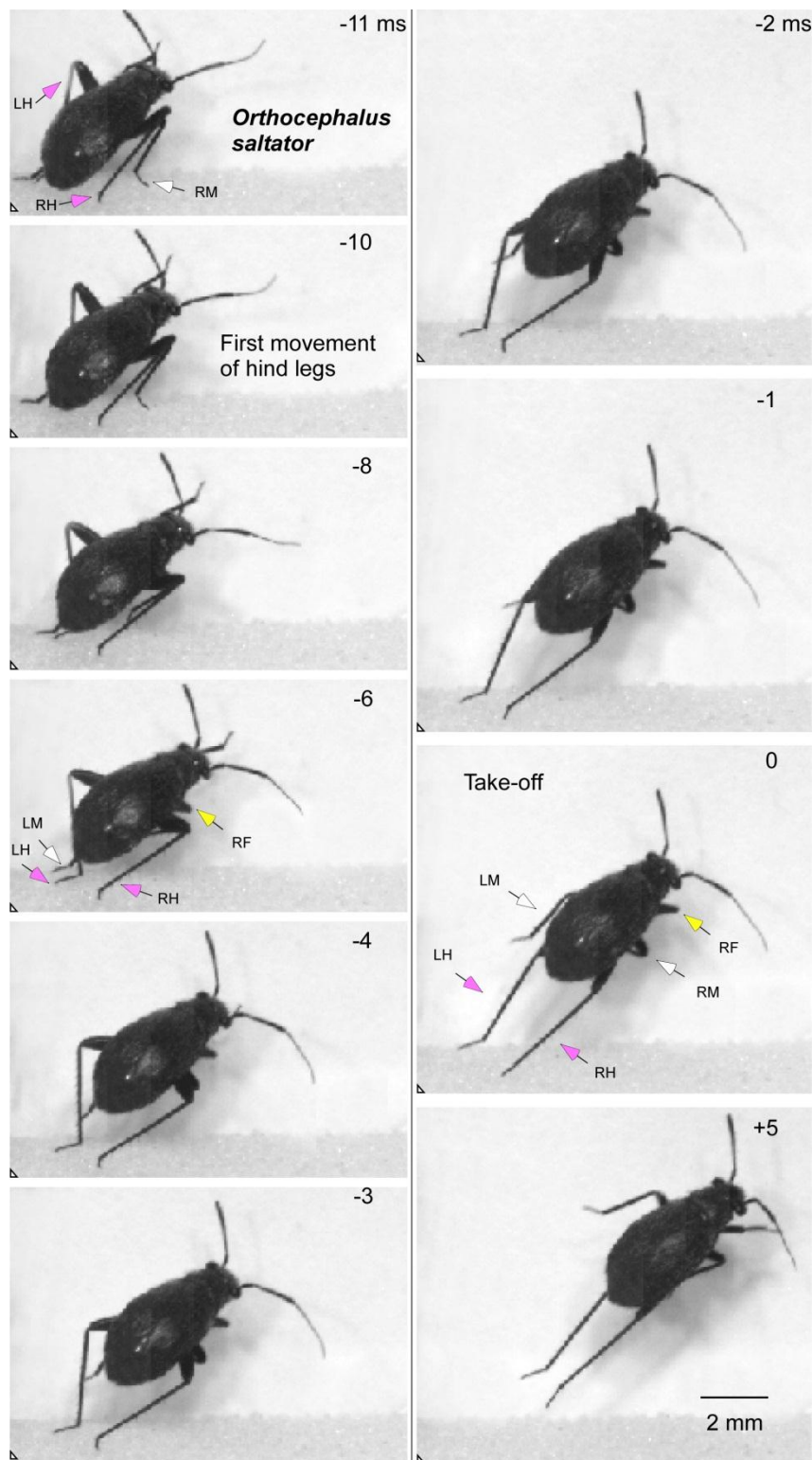


**Fig. 5**

**Jump by a female, macropterous *Microtechnites bractatus* from the horizontal and viewed from the side.** Selected images, captured at a rate of  $1000 \text{ s}^{-1}$  and with an exposure time of 0.2 ms, are arranged in two columns. The first propulsive movements of the hind legs occurred at time -10 ms and the insect became airborne when the hind legs lost contact with the substrate at 0 ms.



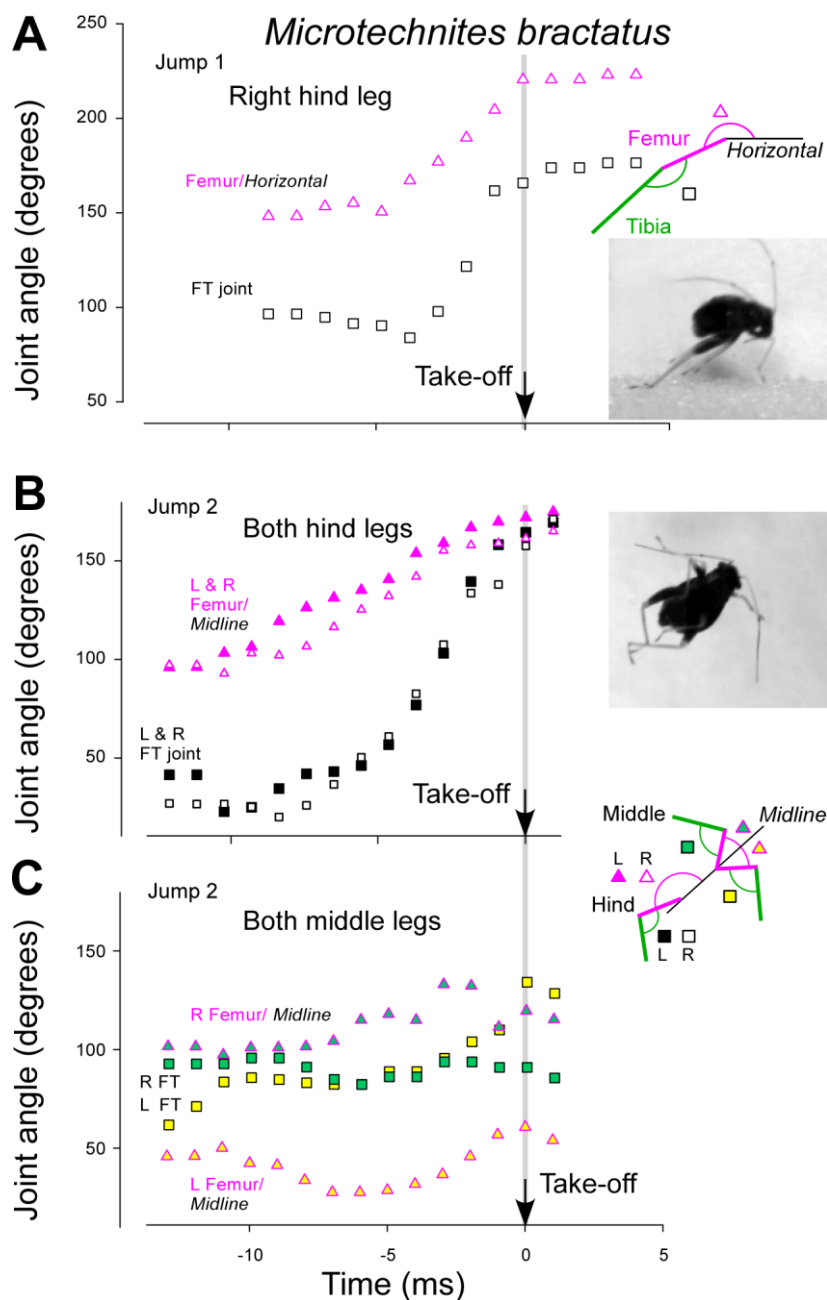
**Fig. 6**  
**Jump by a female, macropterous *Microtechnites bractatus* viewed from underneath.** The insect jumped from the glass front of the chamber and was propelled by the movements of the two hind legs. Images were captured at  $1000 \text{ s}^{-1}$ .



**Fig. 7**

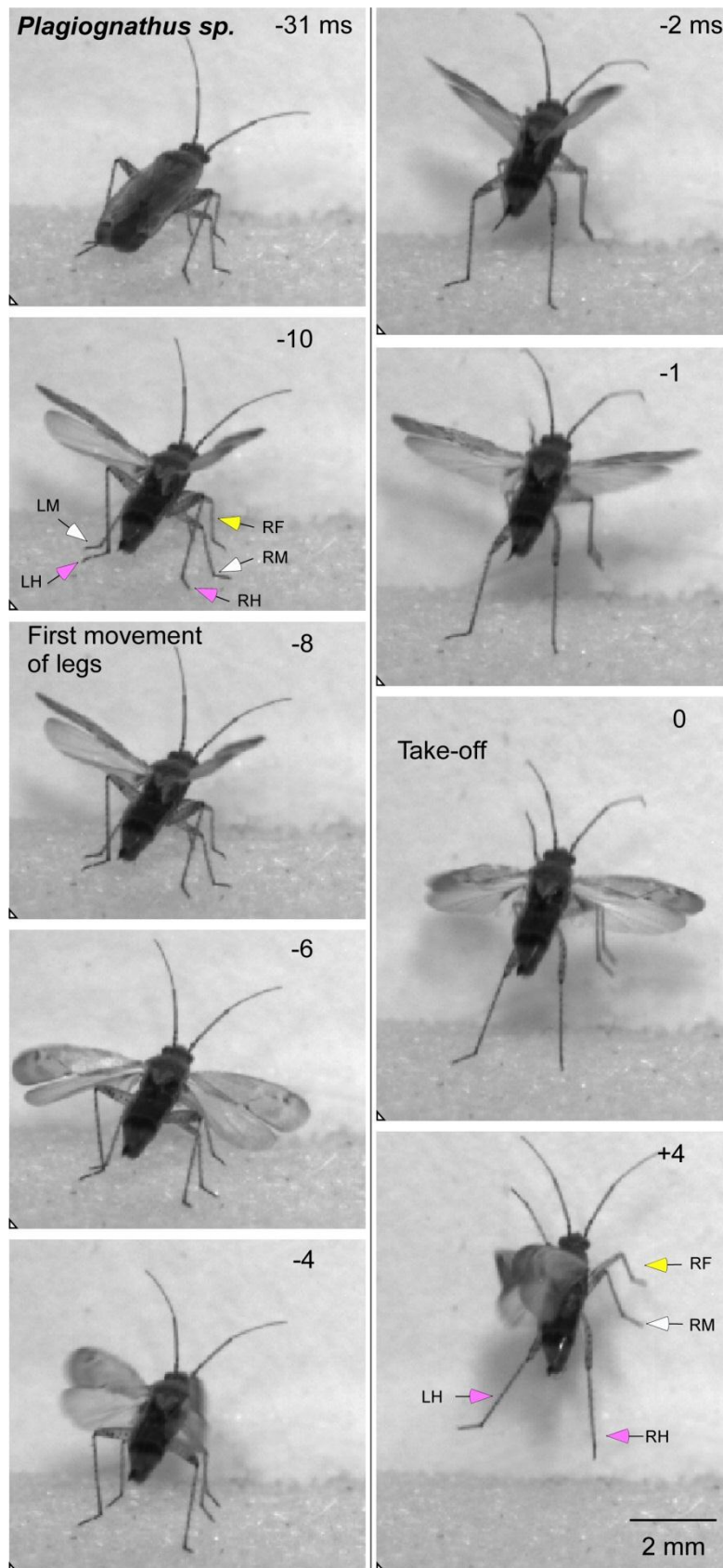
**Jump by a macropterous *Orthocephalus saltator* from the horizontal and viewed from behind.** The front and middle legs lost contact with the substrate at -8 ms before take-off so the jump was then propelled only by movements of the hind legs. Images were captured at  $1000 \text{ s}^{-1}$ .





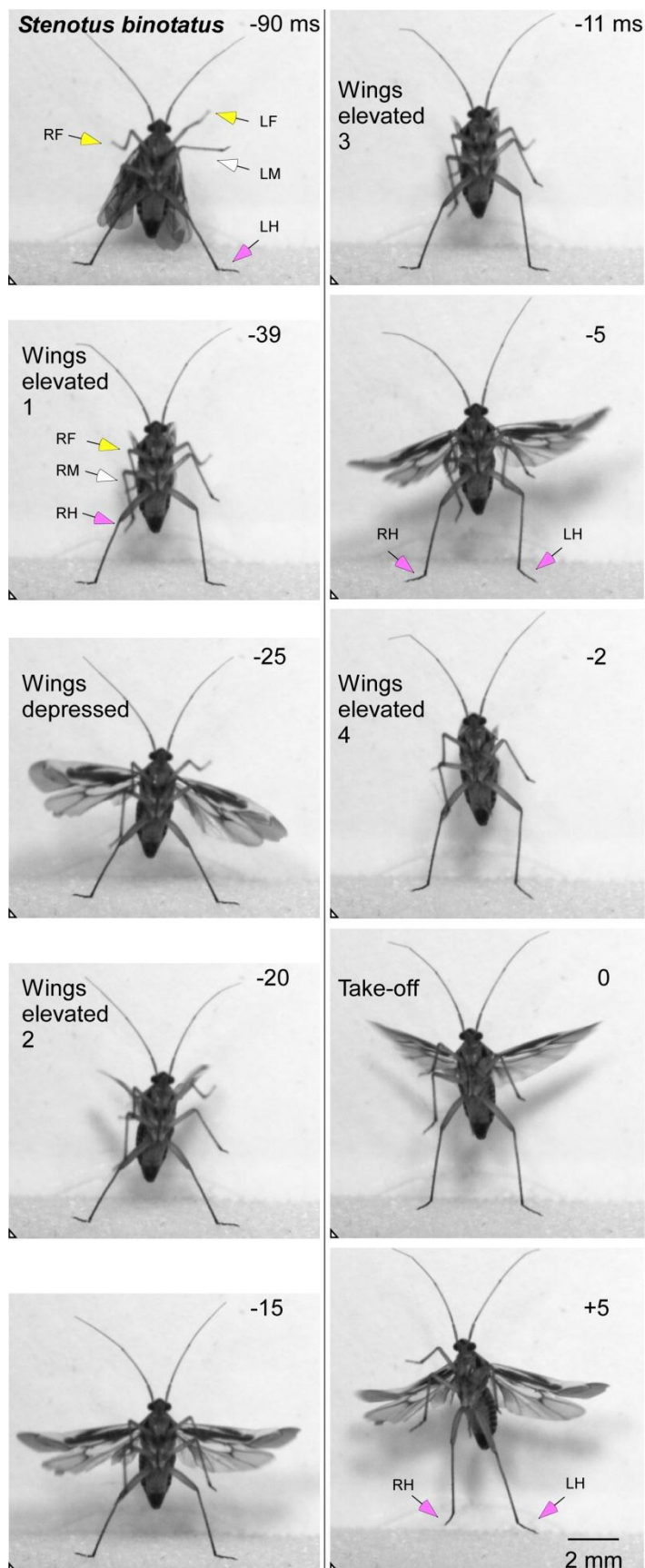
**Fig. 8**

**Changes in joint angles of the propulsive legs during jumps by *Microtechnites bractatus*.** (A) Side view of jump 1 in which the depression of the right hind femur and extension of the right hind tibia are plotted. (B, C) Ventral view of jump 2. (B) The angular changes of the same two joints in the left and right hind legs are plotted. (C) The same jump in which the changes in the angles of the same two joints are plotted for the left and right middle legs. The inset frames from the two jumps and the stick diagrams indicate how the angles were measured.



### **Fig. 9**

**Jump by *Plagiognathus* sp. propelled by leg and wing movements.** The wings opened and then started to depress before the first propulsive leg movement began at frame -8 ms. The wings were then elevated and depressed while the hind legs depressed and extended to propel take-off. Images were captured at  $1000\text{ s}^{-1}$ .



## Fig. 10

**Wing movements alone can propel take-off.** Take-off by *Stenotus binotatus* that started with the hind legs already depressed and extended. No further movements of the middle or hind legs occurred but four cycles of wing movements preceded take-off. Images were captured at  $1000\text{ s}^{-1}$ .

**Table 1. Body form of Mirids**

Body length and mass, and lengths of the hind femora and tibiae (means of means  $\pm$  s.e.m.) are given for five species of mirids. N indicates the number of individuals from which the measurements were taken. The ratios of leg lengths are given relative to the front legs.

	Body Mass, mg	Body Length, mm	Hind leg, Femur, mm	Hind leg, Tibia, mm		Ratio of leg lengths		Hind leg length as % of body length	Hind leg length (mm)/ body mass ^ 1/3 (mg)
					Front	Middle	Hind		
<i>Microtechnites bractatus, female</i> (N=4)	3.4 $\pm$ 0.7	2.7 $\pm$ 0.03	1.4 $\pm$ 0.02	2.0 $\pm$ 0.1	1	1.2	1.9	150	3.3
<i>Orthocephalus saltator</i> (N=3)	4.4 $\pm$ 1.9	3.2 $\pm$ 0.2	1.5 $\pm$ 0.03	2.1 $\pm$ 0.02	1	1.2	1.8	147	3.4
<i>Phytocoris varipes, male</i> (N=5)	7.9 $\pm$ 0.04	5.6 $\pm$ 0.3	2.0 $\pm$ 0.2	2.3 $\pm$ 0.2	1	1.1	1.9	190	5.5
<i>Phytocoris varipes, female</i> (N=5)	12.2 $\pm$ 0.6	6.4 $\pm$ 0.1	1.8 $\pm$ 0.2	2.4 $\pm$ 0.01	1	1	1.9	178	4.8
<i>Plagiognathus sp.</i> (N=16)	2.2 $\pm$ 0.3	3.9 $\pm$ 0.2	1.6 $\pm$ 0.2	2.2 $\pm$ 0.1	1	1.1	1.7	151	3.8
<i>Psallus perissi</i> (N=7)	13.3 $\pm$ 0.8	7.4 $\pm$ 0.1	2.1 $\pm$ 0.1	2.7 $\pm$ 0.1	1	1.1	1.4	88	3.2



**Table 2. Jumping performance of Mirids**

The jumping performance of mirids (mean of means  $\pm$  s.e.m.). N indicates the number of individuals from which the measurements were taken; n indicates the number of jumps. These measurements are shown in columns 2-6 on the left. Columns 7-12 on the right are calculations made from these measurements. The best jumps by an individual, defined by the highest take-off velocity, are also listed.

	Body Mass	Time to take off	Take-off velocity	Take-off angle	Body angle at take-off	Acceleration	g force	Energy	Power	Force	Power/kg muscle
Formula	$m$		$v$			$f = v/t$	$g = f/9.81$	$E = 0.5 m v^2$	$= E/t$	$= m f$	$= \text{power} / (.1m)$
Units	mg	ms	$m s^{-1}$	degrees	degrees	$m s^{-2}$	$g$	uJ	mW	mN	$W kg^{-1}$
<i>Microtechnites bractatus</i>											
Average (N=6, n=9)	$3.4 \pm 0.7$	$8.7 \pm 1.1$	$0.5 \pm 0.1$	$76.1 \pm 21.4$	$46.1 \pm 5.6$	61	6	0.5	0.05	0.2	159
Best	3	6	0.8	60.4	51.3	35	14	2.8	0.5	1.2	547
<i>Orthocephalus saltator</i>											
Average (N=3, n=4)	$4.4 \pm 1.9$	$10.7 \pm 0.9$	$0.5 \pm 0.1$	$60.4 \pm 15.3$	$39.1 \pm 8.7$	43	4	0.5	0.04	0.2	96
Best	8.1	8	0.6	3.4	16.5	76	8	1.6	0.2	0.7	223
<i>Phytocoris varipes male</i>											
Average (N=4, n=16)	$7.9 \pm 0.04$	$15.7 \pm 1.2$	$0.8 \pm 0.1$	$25.6 \pm 6.7$	$24.2 \pm 5.4$	54	5	2.8	1.2	0.4	225
Best	8.6	12	1	47.3	39.1	85	9	4.5	0.4	0.7	394
<i>Phytocoris varipes female</i>											
Average (N=4, n=14)	$12.2 \pm 0.6$	$17.2 \pm 1.9$	$0.8 \pm 0.01$	$33.9 \pm 3.02$	$26.7 \pm 3.4$	47	5	3.9	0.2	0.6	186
Best	11.2	10	1	57.2	32.4	99	10	4.2	0.4	0.9	490
<i>Plagiognathus sp.</i>											
Average (N=16, n=36)	$2.2 \pm 0.3$	$9.5 \pm 0.4$	$0.4 \pm 0.02$	$68.1 \pm 4.9$	$46.2 \pm 4.9$	44	4	0.2	0.02	0.1	82
Best	2.3	10	0.6	84.6	58.4	63	6	1.7	0.2	0.2	198

**Table 3.** Best jumping performance (defined as highest take-off velocity) of insects using direct muscle contractions or catapult mechanisms to power leg movements.

Group	Species	Body Mass	Time to take-off	Take-off velocity	Power/kg muscle
		mg	ms	m s <sup>-1</sup>	W kg <sup>-1</sup>
Direct muscle contractions					
Hemiptera: Mirids					
	<i>Microtechnites bractatus</i> female	3	6	0.8	550
	<i>Orthocephalus saltator</i>	8	8	0.6	220
	<i>Phytocoris varipes</i> male	9	12	1.0	390
Trichoptera: Caddis fly	<i>Mystacides azurea</i>	6	16	0.7	230
Lepidoptera: Moth	<i>Hofmannophila pseudospretella</i> (Burrows and Dorosenko, 2015a)	5.4	22	1.2	310
Neuroptera: Lacewing	<i>Chrysoperla carnea</i> (Burrows and Dorosenko, 2014)	11	19	1.0	270
Mantodea: Praying Mantis	<i>Stagmomantis theophila</i> (6 <sup>th</sup> instar female) (Sutton et al., 2016)	194	39	1.0	90
Phasmatodea: stick insects					
	<i>Sipyloidea sp.</i> (Burrows and Morris, 2002)	164	100	0.8	30
	<i>Timema chumash</i> (Burrows, 2008)	47.5	12	0.9	340
Orthoptera: Bush Cricket,	<i>Pholidoptera griseoptera</i> , female (Burrows and Morris, 2003)	600	33	2.1	100
Diptera: Fly	<i>Hydrophorus albofloreus</i> (Burrows, 2013a)	5.3	11.6	1.6	1150
Catapult mechanisms					
Hemiptera:					
Heteroptera Shore bug	<i>Saldula saltator</i> (Burrows, 2009b)	2.1	3.4	1.8	4500
Sternorrhyncha Psyllid	<i>Psylla alni</i> (Burrows, 2012)	3.6	1.0	2.7	36000
Coleorrhyncha	<i>Hackierella veitchi</i> (Burrows et al., 2007)	1.3	1.5	1.5	7500
Auchenorrhyncha					
Cercopidae: Froghopper	<i>Philaenus spumarius</i> (Burrows, 2006a)	12	0.9	4.7	114500
Cicadellidae: Leafhopper	<i>Aphrophora alnii</i> (Burrows, 2006a)	28.3	1.5	3.4	38500
	<i>Aphrodes makarovi</i> (Burrows, 2007a)	18	2.8	2.9	14000
	<i>Cephalelus angustatus</i> (Burrows and Sutton, 2008)	10	2.0	2.0	10000
Membracidae: Treehopper	<i>Stictocephala bisonia</i> (Burrows, 2013c)	28	3.5	2.7	10400
	<i>Entylia carinata</i> (Burrows, 2013c)	5.3	1.1	2.7	33100
Eurymelinae: Gum treehopper	<i>Pauroeurymela amplicincta</i> (Burrows, 2013b)	23	1.9	2.7	46900
Fulgoroidea: Planthopper					
Issidae	<i>Issus coleoptratus</i> , male (Burrows, 2009a)	22	0.8	5.5	160300
Flatidae					
	<i>Colgar peracutum</i> (Burrows, 2014b)	20	1.8	3.2	29200
Dictyopharidae					
	<i>Dictyophara europaea</i> (Burrows, 2014a)	23	2.4	3.9	48400
Siphonaptera: Flea	<i>Archaeopsyllus erinacei</i> (Sutton and Burrows, 2011)	1.0	1.2	1.9	14000
Mecoptera: Snow flea	<i>Boreus hyemalis</i> (Burrows, 2011)	3.5	6.2	1.0	500
Coleoptera: Flea Beetle	(Brackenbury and Wang, 1995; Nadein and Betz, 2016)				
	<i>Sphaeroderma testaceum</i>	4.5	2.1	1.5	5400

	<i>Chaetocnema aridula</i>	1.4	1.5	1.8	11600
<b>Blattodea: cockroach</b>					
	<i>Saltoblattella montistabularis</i> (Picker et al., 2011)	14	10.6	2.1	1100
<b>Orthoptera</b>					
	<i>Xya capensis</i> (Burrows and Picker, 2010)	8.5	1.8	5.4	42600
	<i>Prosarthria teretirostris</i> male (Burrows and Wolf, 2002)	280	30	2.5	1050
	<i>Schistocerca gregaria</i> (male gregarious) (Rogers et al., 2016)	1500	20-30	3.2	1900

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## SUPPLEMENTARY MATERIAL



### Movie 1

Jump by *Phytocoris varipes* viewed from the side, captured at 5000 frames  $s^{-1}$  and with an exposure time of 0.1 ms and replayed at 10 frames  $s^{-1}$ . See also Fig. 2.



## Movie 2

Jump by *Phytocoris varipes* viewed from underneath, captured at 5000 frames  $s^{-1}$  and with an exposure time of 0.1 ms and replayed at 10 frames  $s^{-1}$ . See also Fig. 3.



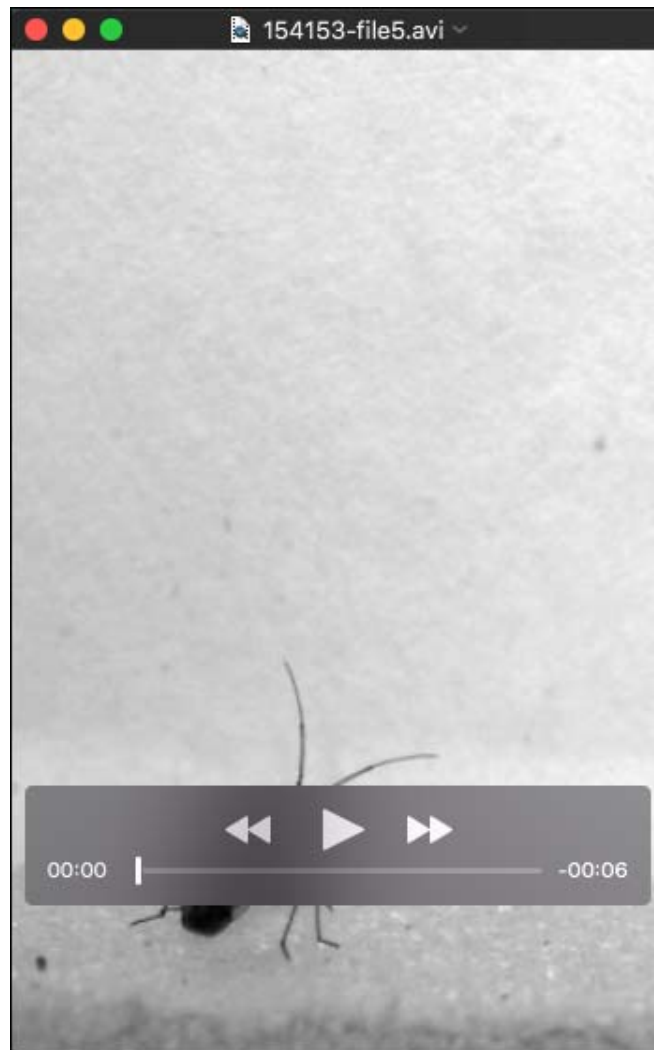
### Movie 3

Jump by *Microtechnites bractatus* viewed from the side, captured at 1000 frames  $s^{-1}$  and with an exposure time of 0.2 ms and replayed at 10 frames  $s^{-1}$ . See also Fig. 5.



## Movie 4

Jump by *Orthocephalus saltator* viewed from behind, captured at 1000 frames  $s^{-1}$  and with an exposure time of 0.2 ms and replayed at 10 frames  $s^{-1}$ . See also Fig. 7.



## Movie 5

Jump by *Plagiognathus* sp. viewed from behind, captured at 1000 frames  $s^{-1}$  and with an exposure time of 0.2 ms and replayed at 10 frames  $s^{-1}$ . See also Fig. 9.